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CRITICAL PERIOD

IN THE

DEVELOPMENT OF THE HORSE.

BY

J. C. EWART, M.D., F.R.S.,

REGIUS PROFESSOR OF NATURAL HISTORY, EDINBURGH.

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INTRODUCTORY.

At a meeting¹ of the Central Veterinary Medical Society of London, at which I exhibited a number of young horse embryos, I had barely time to allude to what may prove a subject of some practical importance, viz., the apparatus provided for nourishing the embryos during the early weeks of development. This apparatus (which consists mainly of what are known as the foetal appendages) I was led to consider from a breeder's point of view by Lord Arthur Cecil asking me, about a year ago, if I could account for so many mares breaking service from the sixth to the ninth week. At the time I could only answer that I agreed with his lordship in believing it was in many cases due to the detachment and escape of an embryo. I have frequently found mares all right, as far as I could judge, at the end of the sixth week, and all wrong some weeks later. This seems to be not an uncommon experience, more especially at the beginning of the breeding season, hence it is always urged by experts that mares should be "tried" frequently during at least the first two months. If holding at the end of the ninth week no further trouble is, as a rule, anticipated. But no one has, as far as I am aware, explained why the breeder experiences so many difficulties during the earlier weeks. According to the evidence obtained by the Royal Commission on Horse Breeding, it appears that about 40 per cent. of the mares selected for breeding fail to produce offspring during any given year. This is a very high percentage

¹ 4th March (see the *Field*, 13th March 1897).

of failure, but from reports recently received it seems to be still higher in certain districts in India.¹ Believing that some of my mares have proved unfruitful for the time being because of their frequently breaking service, and believing further that not a few of the disappointments that fall to the lot of breeders result from the same cause, I decided to examine material collected for another purpose, with a view to shedding fresh light on this difficult but important practical question. To admit of the conditions which obtain in the brood mare being more easily understood, I shall at the outset refer to the apparatus provided for the nourishment of the chick, and to the corresponding structures in one of the simpler mammals.

THE CHICK'S FŒTAL APPENDAGES.²

Every one who has examined a hen's egg at, say, the end of the ninth day of incubation, knows that the already well-formed chick is, as it were, mounted on a large, well-filled forage bag—the yolk sac—from which it hour by hour draws its nourishment. But in addition to the familiar yolk sac there is a second sac, in its way quite as important, though empty of food, viz., the thin compressed sac lying in contact with the shell, which plays the part of a breathing organ or lung. This second sac is known as the allantois. The position and relations of the yolk sac and allantois are indicated in fig. 1. Through the walls of both sacs blood is constantly passing to and from the chick, collecting particles of altered yolk from the one and fresh supplies of oxygen (direct from the air which penetrates the shell) by means of the other. Fig. 1 shows that the chick is connected to the yolk sac by a short thick stalk, and to the allantois by a long slender stalk, and that it is invested by a special water-tight robe

¹ Mr Pease, in his work *Horse-Breeding for Farmers*, says :—"Nine out of ten mares that miss are barren simply from want of care in catching the mare at the right time, or from subsequent neglect;" that "half the mares that are geld are so because the mare, having once or twice refused the horse, she is dismissed from all further consideration," and further, that "many mares will refuse the horse for several successive periods, and then come in season again perhaps without any great show of their condition."

² The chick has been selected not because mammals are related to birds, but that any one desiring to see the fœtal structures dealt with may readily gratify the wish by examining hen's eggs at the ninth or tenth day of incubation.

or inner tunic known as the amnion. The fluid lying between the chick and the amnion (in the dark space in fig. 1) is most useful in preventing jars when the egg is moved, and the thin but tough skin forming the wall of the amnion prevents the chick injuring the yolk sac and allantois. The figure also indicates the position of the air space invariably found, and a portion of the albumen (the white of the egg) which is gradually absorbed as additional nourishment, partly by the yolk sac and partly by the allantois.

THE OPOSSUM'S FŒTAL APPENDAGES.

The young mammal, like the chick, is invested by a fairly tight-fitting tunic, the amnion (*am.*, fig. 2); and, like the chick, it is connected by one stalk to the yolk sac (*y.s.*, fig. 2), and by a second to an allantois (*all.*, fig. 2). But, unlike the chick, the yolk sac in the mammal never contains yolk,¹ and the allantois never plays the part of a simple breathing organ—never, as in the bird, collects oxygen direct from the air. If the yolk sac contains no yolk, and the allantois is unable to expose the foetal blood to the air, how does the embryo mammal live and breathe? In the opossum, and, in fact, in all mammals except the duckmole and echidna, nourishment, at least to start with, is absorbed directly from the uterus into the yolkless yolk sac.² This nourishment, which is partly secreted by uterine glands, is in a sense comparable to the albumen in the bird's egg, and is probably an excellent substitute for the crude material stored up in the yolk sac of birds and lizards. But the embryo mammal not only requires nourishment, it requires to be anchored for a longer or shorter period to the inner wall or lining of the uterus. This fixing is secured in, *e.g.*, the opossum, by means of the thin outer shell-less coat or tunic, which incloses the embryo and all its appendages.

Fig. 2 represents in a diagrammatic way a young American opossum. The embryo, invested by a thin inner tunic, the

¹ The duckmole and echidna are exceptions to this rule, but I agree with Professor Hubrecht of Utrecht in believing that the monotremes are off the main mammalian line.

² The uterus, in which development takes place, being able to provide nourishment, it has been found unnecessary to store up food in a large yolk sac, as in the bird, which for the sake of lightness is almost of necessity oviparous.

amnion (*am.*), has suspended from it a large yolk (*y.s.*) sac and a relatively small allantois (*all.*). Surrounding the embryo and its appendages is an outer tunic, which may be known as the outer embryonic sac (*a, b, c, d*). With part of this embryonic sac the yolk sac blends (from *a* to *c*), and it is through this area (*a, b, c*) the nourishment—the uterine milk—enters, or is absorbed into, the yolk sac. The nutriment is at once conveyed to the embryo by the blood-vessels, which plentifully ramify in that part of the sac which has not fused with the outer tunic. In other words, through the bloodless area (*a, b, c*) nourishment diffuses from the uterus into the yolk sac, thence into the yolk sac vessels, which carry it to the embryo. The embryonic sac does not simply lie in the uterus, it is fixed or cemented, and retained in one definite position. This fixing is mainly secured by cells of the outer tunic in the absorbing area adhering to cells of the uterine lining or mucous membrane. In the opossum and kangaroo and the vast majority of the marsupials these adhesions, at the best very feeble, are in a few weeks broken down, the embryonic sac ruptures, and the embryo, still in a very immature and helpless condition, escapes, and is eventually suspended to a teat, which may or may not project into a pouch or marsupium. It is especially worthy of note that in the opossum the allantois takes no part in securing nourishment from, or in fixing the embryonic sac to, the uterine wall.

THE FETAL APPENDAGES IN THE HORSE.

While opossums and kangaroos and many other ancient and primitive creatures appear on the scene in an immature and helpless condition, some of the higher mammals, more especially some of the members of the hoofed or ungulate tribe, are, as every one knows, at birth so perfect in all their parts that they can at once join and keep pace with the herd to which they by birth belong. Mr Hudson, in speaking of the sheep on the Pampas, says:—"I have often seen a lamb dropped on the frosty ground in bitterly cold windy weather in midwinter, and in less than five seconds struggle to its feet, and seem as vigorous as any day-old lamb of other breeds. The dam, impatient at the short

delay, and not waiting to give it suck, has then started off at a brisk trot after the flock, with the lamb, scarcely a minute in the world, running freely at her side.”¹ One of the most renowned Arabian mares was apparently equally precocious. In *Gleanings from the Desert of Arabia*² occurs the following passage:—“During a short interval of rest, when on a long and rapid journey—her master being pursued—a mare gave birth to a filly foal. He abandoned the foal, and pursued his course on his mare, the dam; when he again halted, he was surprised to find the foal shortly make her appearance.” This foal was placed in charge of an old woman, and was afterwards known as the Keheilet Ajuz, *i.e.*, the mare of the old woman. I have elsewhere³ mentioned that my zebra hybrid “Romulus” was within a minute after birth “rushing about as if he were a young zebra whose existence depended on his at once joining the troop of which his dam was a member.” Even the young hippopotamus is said to be most energetic. On one occasion it is stated a hippopotamus calf, only just born, escaped from its pursuers, and at once made the best of its way to the river.

Are sheep and antelopes and horses throughout their embryonic life nourished in the same way as the young opossum, or is some more effective plan adopted during at least part of the developmental process? I shall now proceed to show that, while at the outset the horse embryo has the same simple apparatus as the opossum, a stage is soon reached when more elaborate and more permanent nutritive appliances are provided. Further, I shall point out that when the new apparatus is being substituted for the old,—when the opossum plan is coming to an end, and the more permanent appliances are barely in working order,—that at this critical period the horse embryo may readily drag its anchors and escape—behave as if it were a young American opossum or an Australian kangaroo.

I shall best accomplish this by describing shortly, and in as simple terms as I can command, the foetal appendages of my five youngest horse embryos.⁴

¹ *The Naturalist in La Plata.* ² Upton. ³ *Veterinarian*, November 1896.

⁴ Since the above was written, I have succeeded in getting a three-weeks' embryo; but for the purposes of this paper, a four-weeks' one is sufficiently young.

The Four-Weeks' Horse Embryo.—Fig. 3 represents in a semi-diagrammatic way, but as near the actual size as possible, a four-weeks' horse embryo and its various appendages and tunics. The embryo, which was found coiled with the tail overlapping the head region, measured just under three-eighths of an inch in length. This embryo, it will be observed, like the chick and opossum, is closely invested by an inner tunic, the amnion (*am.*), and connected by a short stalk with a large yolk sac (*y.s.*). It is also connected by a second stalk (not shown in the figure) with a still relatively small allantois (*all.*). Surrounding and protecting the embryo and its special appendages, is the thin outer tunic (*a, b, c, d*). In the wall of the allantois there are many blood-vessels, and already this sac, by bringing the foetal flood sufficiently near the blood coursing through the uterus, may admit of an exchange of gases taking place—it may, in fact, already play the part of a breathing organ, the oxygen being derived from the maternal blood in very much the same way as in the case of the fish it is derived from the water. As in the opossum, part of the yolk sac (from *a* to *c*) has blended with the outer tunic. Through this bloodless area nutritive material passes into the yolkless sac. With the exception of this bloodless part of the yolk sac, its walls are crowded with blood-vessels. One large vessel which carries blood from the embryo forms a complete circle around the absorbing area; from this circular vessel numerous branches radiate upwards, forming on the way an elaborate network. The blood is eventually collected from this network into two large vessels (veins), which convey it back again to the embryo. As the blood courses through the wall of the yolk sac, some of the nutriment which has entered through the absorbing area (*a, b, c*) is added to it. The yolk sac is thus a reservoir into one end of which nutritive material filters from the uterus, and then diffuses into the vessels of the sac, in order to find its way to and supply the ever-increasing wants of the embryo. As in the opossum, the outer tunic is anchored to the lining of the uterus by some of the cells occupying the absorbing area (*a, b, c*); but, as in the opossum, the connections are easily broken down. This is in striking contrast with what occurs in certain other mammals. In some cases a special uterine pouch is prepared beforehand for each embryo, from which pre-

mature escape is all but impossible. Should one of these embryos succumb in the struggle for life (which often begins before birth), it still remains in its pouch, and is bit by bit absorbed. From first to last in the case of the mare the connections between the embryonic sac and the uterus are, compared even with other ungulates, easily broken down. As I have on several occasions observed, the moment an incision is carried upwards from the neck into the horn of the still contractile uterus, the embryonic sac begins to protrude, and, still entire, the sac may be at once forced, by the contractions of the uncut upper part of the horn, into the body of the uterus. Hence, if the neck of the double horned uterine sac is in a flaccid and unhealthy condition, or if strong wave-like contractions are set up in the uterine horns, there is little chance of a horse embryo only a few weeks old long retaining its position, even if well cemented to the uterine mucous membrane. The need of supplementary anchorages is early recognised in the case of the horse. Even at the fourth week a ring (*an.*, fig. 3), consisting of delicate nearly parallel ridges, exists around the absorbing area. These ridges not only dip into depressions in the lining of the uterus, but in addition many of the cells covering them blend with the adjacent uterine cells. Further, some of the cells forming the outer tunic or embryonic sac increase in length, so as to form an indistinct belt or girdle, nearly on a level with the embryo. This girdle occupies in a section the position indicated by the letters *t.g.*, in fig. 3.

The Five-Weeks' Horse Embryo.—If we turn from the four to the five-weeks' embryo we find various important changes have taken place. The embryo, now five-eighths of an inch in length, has all but lost its gill slits, while a rudiment of the ear has appeared in connection with the remnant of the first cleft; the tail is nearly straight, and, compared with the limbs, relatively shorter than at four weeks, and the limbs seem to contain at their tips rudiments of three separate digits; at four weeks the limbs are quite undifferentiated. In fig. 4, which represents the actual size of the various structures, it will be noticed (1) that while the yolk sac (*y.s.*) is larger, the absorbing area (*a, b, c*) is smaller than at four weeks; (2) that the capacity of the allantois (*all.*) has greatly increased; and (3) that the girdle (*t.g.*) is more pronounced and

nearly equatorial in position. The embryo, doubtless, still obtains its nourishment by means of the yolk sac, but it may be assumed the allantois is indirectly a fairly effective breathing organ. Compared with the chick the development has been slow;¹ but although no great size has been reached, by the end of the fifth week the foundations of the more important organs have been laid. Compared both with earlier and somewhat later periods, the five-weeks' embryonic sac is well fixed to the uterus; for in addition to the adhesions in the region of the absorbing area, and the hold obtained by the plicated ring around this area, there is a very complex and nearly equatorially placed girdle. As the embryonic sac which contained my five-weeks' embryo escaped from the uterus, the girdle appeared as a whitish band nearly a quarter of an inch in width. On section this girdle is seen to consist not merely of elongated cells, as at the end of the fourth week, but of numerous delicate folds separated from each other by deep furrows. That it is concerned in fixing the embryo is evident from the adhesion of uterine cells to its surface.²

When we take into consideration the size, structure, and position of the girdle just described, and of the ring around the absorbing area, it may, I think, be assumed that the horse embryo is more firmly fixed to the uterus at the end of the fifth week than at any subsequent period prior to the development of the numerous processes (villi) which during the eighth week sprout out like so many delicate rootlets from the outer surface of the allantois.

The Six-Weeks' Horse Embryo.—Although the six-weeks' embryo is little more than an eighth of an inch longer than the five-weeks' one,³ it is quite twice as heavy; and though it appears to be

¹ There is not the same urgency to hurry on the development in the mammal as in the chick—an embryo carefully hidden and guarded in a uterus is perfectly safe.

² This girdle (not hitherto found in any mammal), in addition to fixing the embryonic sac, may be the means of absorbing additional nourishment, which may reach the embryo either through the yolk sac or the allantois.

³ During the first seven weeks the amount of nourishment is likely to vary considerably, and the extent of the absorbing area is also likely to vary. Hence in collections of four or five or six weeks' embryos considerable differences in size and extent of development would in all probability be met with. I should not be surprised to find a six-weeks' embryo considerably larger than the one in my possession, or a five-weeks' one somewhat smaller. Further, during the earlier

tri-dactylous, there can no longer be any doubt as to its belonging to the great horse family. The limbs are better formed, and, compared with the tail, relatively longer than at the end of the fifth week. The embryonic sac (*a, b, c, d*), still ovoid, measures three inches in the one direction, and over two in the other, and the allantois (*all.*) has fused with the greater extent of its inner surface. The yolk sac (*y.s.*) has still about the same capacity as at the end of the fourth week, but the absorbing area (*a, b, c*) is only about half the size. The girdle (*t.g.*), equatorial in position at the end of the fifth week, now lies near the pole occupied by the absorbing area.¹ From the absorbing area being comparatively small, and the special fixing structures occupying one pole, I am inclined to think that, about the end of the sixth week, the whole of the embryonic sac might be easily detached. Were it an opossum embryo, preparations would soon be made for its birth. The horse may not have quite forgotten this ancestral habit. About the end of the sixth, as at the end of the third week, the whole reproductive system is in all probability in a somewhat excitable condition. All the physiological changes which occur during oestrus are likely to supervene in a more or less pronounced form about the end of the third and again at the end of the sixth week. In other words, the habit which the nervous and other systems have of becoming periodically excited is not apparently quite thrown off for some weeks after a successful service. In some mammals the nearly-ripe eggs found in the ovary after development has started are said to be absorbed; but in the mare one or more eggs may be matured and discharged several weeks after she has settled. There is a case on record of a mare bringing forth twins, a foal and a mule. She was presented to a jackass fifteen days after being served by a horse. The escape of ova (ovulation) is accompanied with an extra rush of blood to the ovaries and to the uterus, which implies an excited condition of the nervous apparatus of these organs, increased secretion in the uterine glands, and more or

weeks, embryos from small mares are not likely to differ much, if at all, in size, from embryos taken from large mares. My five smallest embryos (four to eight weeks) are from mares from 14.2 to 15 hands high.

¹ In the only six-weeks' specimen I have seen, this girdle was narrow and broken up into short links or segments, as if in process of disintegration.

less powerful contractions of the numerous uterine muscular fibres. The periodic disturbance is likely to be greater in mares which have not previously bred. In mares which have had several foals, or have recently foaled, the uterine vessels are readily enlarged, and from the first tend to deflect blood which might otherwise rush to the ovaries. At a time when the connections between the embryonic sac and the uterus are at their weakest, this extra excitement of the reproductive system may very readily lead to an arrest in the developmental process, and eventually to the embryo being discharged. When this happens, evidence will soon be forthcoming that the mare has broken service.

The Seven-Weeks' Horse Embryo.—If the storms which naturally set in about the end of the sixth week are successfully weathered, a period of calm sets in, not likely to be seriously interrupted at the end of the ninth week; for by that time the uterine vessels will have sufficiently increased to carry off all the extra blood that finds its way to the reproductive organs. The ovaries will thus be but little excited, and the nervous system, as a whole, will all but maintain its normal calm. There is, however, another danger ahead, for at the end of the seventh week the supply of nourishment by means of the yolk sac has all but come to an end, and the arrangements for providing for the wants of the embryo, by means of the allantois, have not yet been completed. To put it another way: at or about the end of the seventh week the remote marsupial ancestors of the horse were, in all probability, in the habit of leaving the uterus for the shelter of the pouch or marsupium, already capable of imbibing ordinary milk from teats, instead of absorbing uterine milk by means of a yolk sac.¹ The seven-weeks' embryo (with its appendages and its inner and outer investing tunics) is represented in fig. 6. This embryo, which is nearly half an inch longer than the six-weeks' one, is at a most interesting stage in its development. Had it been an opossum, it would have already been glued to a teat in the marsupium,—not yet able to suck, but sufficiently

¹ Some would even go the length of saying that, in obedience to the law of heredity, there is an attempt on the part of the horse embryo, at or about the end of the seventh week, to slip its moorings and escape from the uterus,—to make an attempt to repeat this particular episode in the ancestral history.

advanced to admit of milk being pumped from the mammary glands into its gullet or œsophagus. The figure indicates the exact size (just under $1\frac{1}{4}$ inches) of the embryo. The open mouth and well-formed lips and tongue seem to indicate that it is quite ready (should a huge reversion or throw-back take place) to receive and hold on to a teat. There is, in fact, in the seven-weeks' embryo not a little in favour of the view that all animals climb their own ancestral tree,—that there is a more or less accurate recapitulation by each individual of the entire ancestral history.¹ I have no doubt the remote ancestors of the horse were born ere this stage was reached. If the rate of progress was the same in the remote past as it is now, the birth would originally occur on the forty-seventh or forty-eighth day. As the figure shows, the head is less flexed than at six weeks, and the nose, eyes, and ears are better formed, and that it is beyond doubt a mammalian embryo is proved by the presence of rudiments of hair on the snout and eyelids. But any embryologist would not only at once place this embryo in the mammal group, he would have no hesitation in asserting it belonged to the horse family. The fore and hind limbs clearly point to this, for already the frog is partly modelled, and the fetlock is quite distinct; and while the position of the knee and elbow are evident in the fore limb, the position of the hock and stifle are equally evident in the hind; and, further, the possibility of having more than one complete useful digit for each foot no longer exists. Moreover, even without the aid of a lens, two teats can be detected, and hence it would be possible, without knowing anything of the history of this embryo, to state that it had been obtained from some member of the horse family, and that it would probably have developed into a filly foal.

On turning to the appendages, it will be observed that though the yolk sac has lost little in capacity, its connection with the embryonic sac has been considerably reduced. The absorbing area is now very small (*a-c*, fig. 6), so small that it is difficult to understand how sufficient nourishment has been obtained to

¹ That there is not an exact, or anything approaching an exact, recapitulation, a glance at the seven-weeks' embryo will at once show. The remote ancestors had five complete digits, but even in the seven-weeks' horse there is no external indication of more than a single digit for each foot.

admit of so much growth during the seventh week.¹ But while there has been little change in the yolk sac, the allantoic sac (*all.*) has now about three times the capacity it had at six weeks. Whether the blood, as it circulates through the allantois, collects nutritive material as well as fresh supplies of oxygen, I am not yet able to say. The changes in the outer cells of the embryonic sac are more interesting and suggestive than those in the yolk sac and allantois. The ring (*an.*) around the absorbing area, though flattened, still consists of delicate ridges. The girdle, still circular at six weeks, has been folded so as to assume an extremely irregular form (*t.g.*, fig. 6). The outer margin of the girdle consists of complex prominent ridges, which fit into corresponding grooves in the uterine mucous membrane. These ridges extend some distance along the main trunks of the vessels passing to and from the allantois. Part of the space within the folded girdle is occupied by numerous delicate ridges, which also doubtless help in retaining the embryonic sac in its place. Up to this time the embryo is suspended by means of the yolk sac from the upper wall of the uterus. Hence all these ridges and processes fit into grooves and depressions in the mucous membrane lining the roof of one of the uterine horns.²

In the six-weeks' embryo the cells of the outer tunic beyond the girdle are unaltered, but at the end of the seventh week this tunic presents a countless number of minute dots. These dots (*t.t.*), which are due to the elongation of small groups of cells, are the first indication of the coming nutritive processes or villi. Later a villus sprouts out in the position of each dot, the cells of the tunic forming a covering for the allantoic outgrowth in very much the same way as the finger of a glove covers a finger. Whether these minute patches of elongated cells at the end of the seventh week assist in taking in nourishment, and also in fixing the embryonic sac, further investigations will doubtless reveal. The interesting point to notice is that the rudiments of

¹ Although the absorbing area is small at the end of the seventh week, the yolk sac contains countless numbers of minute granules, which are doubtless of nutritive value.

² Usually the embryo, to start with, in the mare occupies the right horn, with its head nearest the body of the uterus. Later, part of the embryo may lie in the enlarged body of the uterus; but the hind limbs remain to the last in the right horn.

the more permanent structures (the villi) concerned with the nourishment of the embryo have appeared before the end of the seventh week. Much must depend on what happens during the beginning of the eighth week. If the embryo has been developing in a normal fashion, and is sufficiently vigorous, villi will sprout out from every part of the now extensive allantoic sac, and each villus as it grows will receive a covering of cells from the outer tunic. If the lining of the uterus is in a healthy and sufficiently vigorous condition, it will provide pits for the villi as they develop.

When the villi actually begin to grow is not yet known; but though small and simple, they are well formed, and present in countless numbers at the end of the eighth week. Once established, they increase in size and complexity (7^b , 7^c), which implies they become more and more capable of obtaining a plentiful supply of nourishment, and of fixing the ever expanding sac containing the embryo to the lining of the uterus.

It is hardly necessary to explain that when an embryo is at last provided with a countless number of allantoic villi, it is in an infinitely better position than when its only means of obtaining supplies was a small porous area through which nutriment filtered from the cavity of the uterus. Each villus may be compared to a delicate branching rootlet, only it has the advantage (1) of having blood rapidly circulating through its various branches, by which the nutriment collected is conveyed at once to the embryo, and (2) of having a relatively enormous amount of a highly nutritive fluid—the maternal blood—brought sufficiently near to admit of the materials required for building up the bones and muscles and other parts of the embryo being readily absorbed. But the villi may be said to play the part of leaves as well as roots, for they admit of an exchange of gases. Through them the foetal blood gets rid of its poisonous carbonic acid, and at the same time secures a fresh supply of oxygen, without which tissues can neither be built up nor maintained. When the villi begin to act is not yet known. Though still very small, they are quite visible to the naked eye at the end of the eighth week. If we suppose they are fairly efficient by the middle of the eighth week, it will be evident, if the seven-weeks' is compared with the eight-weeks' embryo (fig. 7), that they are infinitely more

efficient than the primitive apparatus in operation during the earlier weeks.

The Eight-Weeks' Horse Embryo.—This embryo is twice the length and four times the weight of the seven-weeks' embryo. As fig. 7 shows, at eight weeks we have a miniature horse. The mouth is now closed, the eyes are provided with eyelids, the ear projects some distance from the head, and the tail, compared with the legs, is relatively short. The amnion (*am.*) still forms a complete robe or mantle, and, by means of the fluid it contains, to the last is of the utmost use both for the protection of the foetus and the dam. The two stalks—yolk and allantois—have already blended for some distance (*sta.*), but the yolk sac (*y.s.*), though now of little or no use, still persists.¹ The absorbing area (*a-c*) is very small, but still surrounded by a prominent ring (*an.*), external to which the girdle (*t.g.*) may still be seen. The allantoic sac is considerably larger than at seven weeks, and there projects from it a countless number of villi. Some of these villi are represented, but on too large a scale, in fig. 7 (*all. villi*). The majority of them are still simple processes, but in a few branching has already set in. As they increase in size they form miniature vascular trees (7^b, 7^c), which occupy equally complex pits in the lining membrane of the uterus.² That the new mode of catering for the wants of the embryo is an efficient one will be still more evident when I mention that a four-months' embryo, *i.e.*, an embryo twice the age of the one represented in fig. 7, may be over ten inches in length.

Having shortly described the foetal appendages of four horse embryos, I trust those interested in the development of the horse will now be better able to realise the conditions under which the embryo lives during the earlier weeks, the provisional and more permanent arrangements for its nourishment, and especially that a critical stage is reached as the yolk sac ceases to convey nutriment, and the allantoic villi come into action. As I have found breeders and others practically interested in our domestic animals only too glad to learn all that science has to say on

¹ At six months the yolk sac has about the same capacity as at six weeks, but it is folded longitudinally, and completely concealed in the umbilical cord.

² The villi in the mare are never more than an eighth of an inch in length, and at birth they are simply withdrawn from their pits.

problems which have long been puzzling them, and sometimes urgently pressing for solution, there is no apology needed for having treated this subject on strictly scientific lines.

SUMMARY.

I have endeavoured to show that the horse embryo, like the young opossum, is inclosed by a special inner tunic (the amnion), and provided with a pair of appendages (the yolk sac and the allantois), and, further, that a thin outer cellular tunic (the embryonic sac) completely envelops the embryo and all its belongings. The fluid which fills up the space between the embryo and the amnion forms a sort of water-jacket, which is doubtless most useful alike for the protection of the embryo and its dam. The yolk sac, unlike the corresponding structure in the chick, is empty, for the simple reason that there is plenty nourishment available in the uterus or in the blood abundantly coursing through its walls. The more readily to secure this nourishment, part of the yolk sac fuses with the outer cellular tunic to form a sort of filter, through which the nutriment enters the originally empty sac. The nutritive material, after it may be undergoing some chemical change, finds its way from the cavity of the yolk sac into the blood-vessels which ramify in its wall as far as the edge of the filter or absorbing area.

In the opossum, and the vast majority of the marsupials, the young are born in a very immature condition—as soon as they are able to seize and hang on to the teats. These ancient forms have not discovered that, by utilising the allantois (originally a breathing organ), they might considerably prolong the protection afforded by the uterus;¹ that when the yolk sac fails, by throwing out root-like processes from the allantois, they might tap an almost inexhaustible food supply. But all the higher forms (the Eutheria) utilise the allantois, and some of them are already so perfect at birth that the time may come when the milk glands (very old-fashioned organs), so essential to the marsupials, may in some cases be entirely, or almost entirely, dispensed with.

¹ The Bandicoot is the only marsupial in which the allantois has been shown to take part in nourishing the embryo.

In the case of the horse, the yolk sac ceases to provide a sufficient supply about the end of the seventh week; but the embryo, instead of being born at this period, has the new and more efficient nutritive structures provided—the allantoic villi.

During the first seven weeks the embryo is fixed to the lining of the uterus by means of the embryonic sac. In the region of the absorbing area some of the foetal cells blend with the adjacent uterine cells. Around the absorbing area a circular adhesive ring is formed. This ring shrinks as the absorbing area diminishes. A supplementary grappling apparatus appears in the form of a girdle, which becomes, up to the seventh week, more and more complex, and travels towards the ring just mentioned as the allantois increases in size.

The allantois, a simple breathing organ in the chick and young reptile, is probably concerned in the aeration of the blood from an early period—the third or fourth week—in the horse. But by the end of the seventh week minute patches of enlarged cells belonging to the outer tunic indicate that allantoic outgrowths will soon appear, and by the end of the eighth week thousands of villi have sprouted out from its surface, and are already lodged in minute pits specially formed in the lining of the uterus. These villi not only procure nourishment and fresh supplies of oxygen, they further fix more or less firmly the embryonic sac to the wall of the uterus.

At the end of the third week of gestation, when the reproductive system passes through one of its periods of general excitement, about one-fourth of the embryonic sac probably adheres to the uterus; but at the end of the sixth week, when another wave of disturbance arrives, all the grappling structures are at one pole. Hence there is probably more chance of the embryo "slipping" at the end of the sixth than at the end of the third week. About the end of the seventh week the supply of nourishment by means of the yolk sac is coming to an end, and there is perhaps still about this time a hereditary tendency for the embryo to escape. Unless the new and more permanent nutritive apparatus is provided, unless a countless number of villi rapidly sprout out from the allantois, the embryo will die from starvation during the eighth week, and in a few days be discharged.

It may therefore be taken for granted that there is a certain amount of danger at the end of the third and sixth weeks, but that the most critical period is about the end of the seventh or beginning of the eighth week ; for unless the villi appear in time and succeed in coming into sufficiently intimate relation with the uterine vessels, the developmental process is of necessity for ever arrested.

CONCLUDING OBSERVATIONS.

Evidently, from what I have already stated, breaking service may be due either to abnormal development of the embryo or to its surroundings being unsuitable.¹

Nature may be said to have provided against what we call breaking service. When one thinks of the millions of eggs produced in a single season by the cod and certain other fishes, one is apt to suppose that there is no relation between the number of ova and the wants of the species. On the other hand, the solan goose lays but one egg a year, and the elephant may not mature a score of eggs in a hundred years. I believe a mare may ripen and shed from ten to twenty eggs during the year. If this is the case, bearing in mind that the period of gestation is eleven months, evidently in the mare provision has been made against accidents during the earlier weeks of the breeding season. Considering first how the embryo may be concerned with breaking service, I may point out that if the egg or the sperm has been insufficiently nourished, or, it may be, over nourished, the segmentation of the egg may be abnormal ; or, if this is successfully accomplished, a feeble embryo may be the result—an embryo with, it may be, a small allantois, or with an imperfect yolk sac circulation, or an embryo incapable of anchoring itself to the lining of the uterus. Or the embryo may reach the seventh week, but either because the allantois is insufficiently developed, or because it lacks the energy required to throw out the all-important villi, the more permanent relations may never be

¹ In discussing this subject it will be best to take for granted that the mare has settled, and held at least beyond the third week. It would be useless to include mares which have never settled when dealing with this subject.

established, with the result that it is sooner or later discharged. Hence the necessity of having vigorous germinal cells to start with—in other words, of the breeding stock being in a healthy and vigorous condition ; for whether it is or is not possible to transmit acquired characters, it is certainly possible, by means of unsuitable surroundings and injudicious feeding, to diminish the vitality of both the eggs and sperms.

With regard to the immediate surroundings of the embryo, probably the conditions are oftenest rendered unsuitable for the development of the embryo by an unhealthy state of the uterine mucous membrane. The uterine secretions may be acid instead of alkaline (they are said to be acid in mares that have frequently broken service ; acid secretions destroy the sperms as they pass upwards through the uterus), excessive or the opposite. They may, on the one hand, be unsuitable for the due nourishment of the embryo, or they may prevent it being properly fixed. At a later period, by accumulating between the basis of the villi, the secretions may actually dislodge them from their pits. But even should the mucous lining of the uterus be normal, neither too congested nor too anæmic, nor yet too irritable, the muscular fibres which enter so abundantly into the uterine wall may be out of order, or the nerves supplying them in a state of unrest. The fibres in the neck and body of the uterus may be relaxed or wanting in tone, or the fibres of the horns, or it may be of the whole organ, may be subject to frequent spasmodic contractions. Whether such contractions result from local irritation or general nervous excitement, if excessive and long continued, the chances of the embryo being long retained will be extremely small.

The question now arises, can anything be done to prevent mares breaking service ? In dealing with the horse, the fact must never be lost sight of that he is an extremely high-strung animal, liable in a panic to completely lose the little self-control he has inherited from his wolf-worried ancestors. This nervousness, which was his salvation when in a wild state, has in some respects been increased rather than diminished by the unnatural life it is now his lot to lead. The horse has strong likes and dislikes, and frets often when separated from his companions. This being the case, it will be easily understood that sudden changes—changes

of temperature, of food, of companions, changes of his surroundings or environment generally, will greatly influence mares, more especially at the breeding season.

It is well known that changes influence more or less markedly all kinds of animals. A change from one country or one district to another may, *e.g.*, lead to increased fertility, or it may result in complete sterility. This is doubtless because the reproductive system is extremely sensitive to changes of every kind. In several cases mares which I received from a distance required several months to adapt themselves to their new conditions, and in all cases the reproductive system was the last to assume its normal state. But what bearing has this on the subject in hand? It all points to a very careful and thoughtful treatment of mares at the beginning of the breeding season. For example, now (April) that the grass is coming on, I might have several mares mated with my zebra—mares which have been under cover and generously fed during the winter,—and then turned out to grass in the same field. The change from the loose-boxes to the field would be nearly as great as from the South of England to the Pentlands, and if the reproductive system is most sensitive to changes, the chances would be strongly against their settling. But even if proof against the effects of substituting an outdoor for an indoor life, turning them one by one immediately after mating would be most unwise. Some mares, even when in foal, “tease” other mares as persistently as a horse. In this way, the excitability which should be allayed, or at least allowed to subside, might be kept up if not exaggerated. At the beginning of the breeding season changes of food, of temperature, and of the surroundings generally should be made as carefully and judiciously as possible; and during at least the first two months after service the mares should neither be over-excited nor over-exerted, neither chilled nor over-heated, neither over nor under-fed, and, in fact, all extremes should be carefully avoided; and it should be remembered that drugs readily reach, and may profoundly influence, even young embryos.

If in this case being forewarned is to be forearmed, some good may result from the conditions under which the horse embryo exists during the early weeks of development having been shortly explained. The practical application of the facts

established may well be left to breeders and veterinarians. I may, however, in conclusion, make the following suggestions:—

1. That mares which have been indoors during the winter, and which are to run at grass during the summer, should be, as it were, acclimatised before they are served, *i.e.*, they should be allowed to run out night and day for two or three weeks, in order to have time to adapt themselves to the change of food, the somewhat marked variations of temperature, and to their new surroundings generally.

2. That mares, more especially excitable ones, should be served in the evening, and shut up apart from other mares or geldings during the night. They should then, until the periodic disturbance has subsided, be kept in a paddock as far removed as possible from mares or geldings likely to tease them.¹

3. That when any signs of œstrum are detected in a mare (whether she has been previously presented to the horse or not), she should be removed from mares believed to be already in foal.

4. That each mare should be carefully watched from week to week, and periodically—every ninth or tenth day—tried until the critical period has been successfully passed.

5. That mares backward and out of condition in the spring should be allowed for some weeks oats at least once a day; for unless they are in a healthy and vigorous state, ova may not be discharged until the summer is well advanced; or, if ovulation takes place, the eggs may be so impoverished that the embryo may fail to survive the critical period, or, if it succeeds in this, develop into a small, weedy foal. It is all but impossible, apparently, for a mare to produce strong, vigorous twins capable of eventually reaching the size of their parents. This is evidently a matter of nourishment. Hence, if the dam is out of condition, or if the foetal circulation is weak, or the allantoic villi in any way unsatisfactory, the foal, if born alive, is not likely to be a source of credit or profit to the breeder.

¹ This year a very healthy, well-bred, cream-coloured mare, though repeatedly served by the zebra during the months of March, April, and May, did not settle. She was again served by the zebra on the 23rd and 25th of June, and then placed in the hands of a breaker, so that she might, if necessary, be sold. I have every reason to believe she is now (July 1897) holding. Probably we were at last successful, because this mare was taken in from grass and kept regularly at work.

DESCRIPTION OF THE FIGURES.

FIGS. 3-7. Natural size; the appendages are represented in section, and are semi-diagrammatic.

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| <p><i>el</i>, Outer embryonic sac or tunic.</p> <p><i>a, b, c</i>, Absorbing area (yolk placenta), consisting of cells (trophoblastic) of the embryonic sac, and of the inner (hypoblastic) cells of the yolk sac.</p> <p><i>an.</i>, Section of ring (annulus) surrounding absorbing area.</p> <p><i>t.g.</i>, Girdle (trophoblastic), formed entirely by a modification of the outer cells of the embryonic sac.</p> <p><i>am.</i>, Amnion—the amnion eventually blends with the allantois.</p> <p><i>all.</i>, Allantois—the stalk connecting the allantois with the embryo is only shown in figs. 1 and 2.</p> <p><i>all.</i>¹, Allantois completely fused with the embryonic sac, which provides a covering for the allantoic villi.</p> <p><i>all.</i>², Allantois in connection with the amnion.</p> <p><i>all.</i>²-<i>all.</i>⁴, The part of the allantois in connection with the yolk sac—in the fifth to the eighth week embryos this</p> | <p>part of the allantois carries non-vascular villi (<i>c.v.</i>).</p> <p><i>all. villi</i>, Allantoic villi, each with a covering derived from the embryonic sac.</p> <p><i>c.v.</i>, Villi (coelomic) lying between the allantois and yolk sac. These internal villi are naked (not invested like the external villi), and are non-vascular; they have not hitherto been found in any mammal, and their function is unknown.</p> <p><i>sta.</i>, Part of the umbilical cord within the amnion formed by the junction of the allantoic and yolk stalks, and containing the main trunks of the allantoic and yolk sac vessels.</p> <p><i>v.</i>, These dots indicate that the greater part of the wall of the yolk sac is vascular.</p> <p><i>v.</i>¹, These dots indicate that the allantois is vascular throughout its whole extent.</p> <p><i>v.</i>², Allantoic vessels, from which branches pass into the villi.</p> <p><i>y.s.</i>, Yolk sac.</p> |
|--|---|

FIG. 1. The hen's egg at the ninth day of incubation. The embryo is connected by a short stalk to the *yolk sac*, which contains nearly all the food required during the developmental process. The additional nourishment is provided by the *white* or albumen which surrounds the yolk. The *allantois* at an early stage grows out from the intestinal tract, becomes extremely vascular, and plays the part of a breathing organ. Numerous vessels are also formed in the wall of the yolk sac; the dots are intended to indicate that the yolk sac and allantois are vascular. The shell is lined with a thin membrane. At one end this membrane is separated from the shell, leaving a space—the air chamber. After Milnes Marshall.

FIG. 2. Represents a young opossum and its foetal appendages. The wall of the yolk sac (*y.s.*) is vascular as far as the circular blood vessel (*s.t.*, sinus terminalis). In the area *a, b, c*, the yolk sac blends with the outer embryonic sac. Through

this area the cells (trophoblastic) of the outer sac are modified so as to assist in taking up nourishment—the uterine milk—from the uterus, and in fixing the embryo during its uterine development. The allantois (*all.*) never reaches the outer sac. It is vascular, and serves only as a breathing organ. After Osborn and Selenka.

FIG. 3. A semi-diagrammatic representation of a four-weeks' (28 days) horse embryo and its foetal appendages. The embryo, which is curved so that the tail lies under the head, measures nearly three-eighths of an inch in length. The limbs are represented by lobes entirely composed of cells, *i.e.*, the rudiments of the limb skeleton have not yet appeared. Behind the head are three arches and three clefts, but the clefts do not appear to open, as in fishes, into the pharynx. The amnion (*am.*) surrounds the embryo, and two stalks proceed from the under surface. The stalk proceeding to the left side connects the embryo with the yolk sac (*y.s.*), the stalk passing to the right contains the vessels of the allantois. The allantois (*all.*) is already in contact with the embryonic sac (*d*), and with the amnion, and it has many vessels (*v*¹) in its wall. The yolk sac is vascular (*v.*), as far as the circular blood-vessel (*s.t.*), and crowded with granules which have entered by the absorbing area (*a, b, c*). The cells of the outer tunic at *t.g.* (on a level with the growing point of the allantois) have undergone considerable elongation, while the cells in the area (*a, b, c*) have given rise to a number of irregular ridges and processes.

FIG. 4. Represents a five-weeks' (35 days) embryo. Note that the absorbing area (*a, b, c*) is smaller than in the 28 days' embryo, while the capacity of the allantois is greater. Delicate villi (*c.v.*) now project from the allantois towards the yolk sac, and the girdle (*t.g.*) now consists of distinct nearly parallel ridges, with furrows between—these ridges, as well as the ridges of the ring (*an.*) around the absorbing area, have been exaggerated in the drawings.

FIG. 5. The 42 days' embryo and its appendages. Note especially that the girdle (*t.g.*) lies near the absorbing area (*a, b, c*), and that the allantois is now a relatively large sac in contact with the greater extent of the outer tunic, and surrounding the greater part of the yolk sac.

FIG. 6. The seven-weeks' (49 days) horse embryo. Contrast this with the other embryos, more especially with the five and

eight weeks' embryos. Note that while the yolk sac has remained almost stationary, the absorbing area has diminished, while the capacity of the allantois (*all.*) has greatly increased. The villi (*c.v.*) extending from the allantois towards the yolk sac are numerous, long and slender, but still devoid of blood-vessels. Indications of the coming external vascular villi occur in the form of minute dots (*t.t.*) over the surface of the embryonic sac. The yolk-sac and allantoic stalks have already united at their inner or proximal ends.

FIG. 7. Represents an eight-weeks' (56 days) horse embryo suspended in the amniotic cavity, and bathed by the amniotic fluid. The embryo is connected with the yolk sac (*y.s.*) and the allantois (only part of which is shown) by relatively large blood-vessels. These vessels and their investing tissues form the proximal part of the umbilical cord (*sta.*). The yolk sac, though having still as great a capacity as formerly, is folded longitudinally, so as to occupy a comparatively small space. Note that the absorbing area is now very small, and especially that numerous simple villi now project from the surface of the embryonic sac. Each villus consists of a vascular allantoic core, and a thin capsule derived from the embryonic sac. The villi are represented on too large a scale, but the embryo and yolk sac are natural size.

7^a. Represents three villi from an eight weeks' embryo.

7^b. A single villus from a sixteen-weeks' embryo, and

7^c. A single villus from a twenty-four-weeks' embryo—all thirty times natural size.

The villi fit into pits or moulds in the lining of the uterus. As the foetal blood circulates through the villi it comes sufficiently near the maternal blood circulating through the wall of the complex pits or moulds to admit of an exchange of fluids and gases—the foetal blood transfers its excess of carbonic acid to the maternal blood; while the maternal transfers to the foetal blood some of its oxygen, and also fluids containing all the ingredients required for the development and growth of the embryo. There is, however, no actual mixing of the maternal and foetal blood. At birth the foetal villi are simply withdrawn from the uterine pits. The villi and pits together are generally spoken of as the Placenta.

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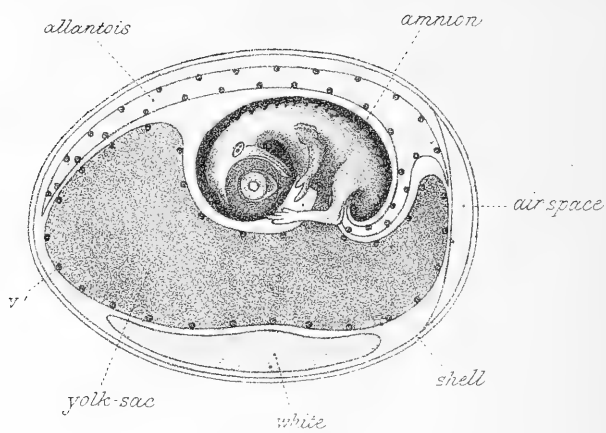


Fig. 1.

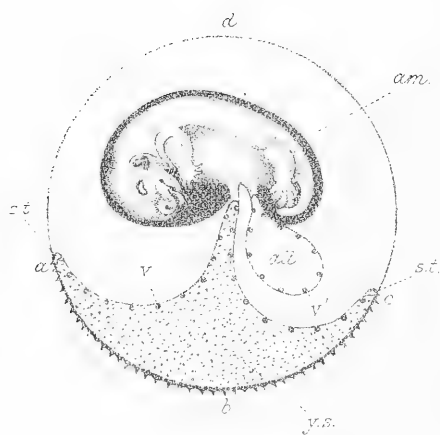


Fig. 2.

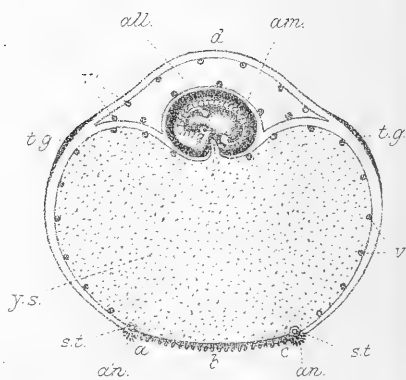
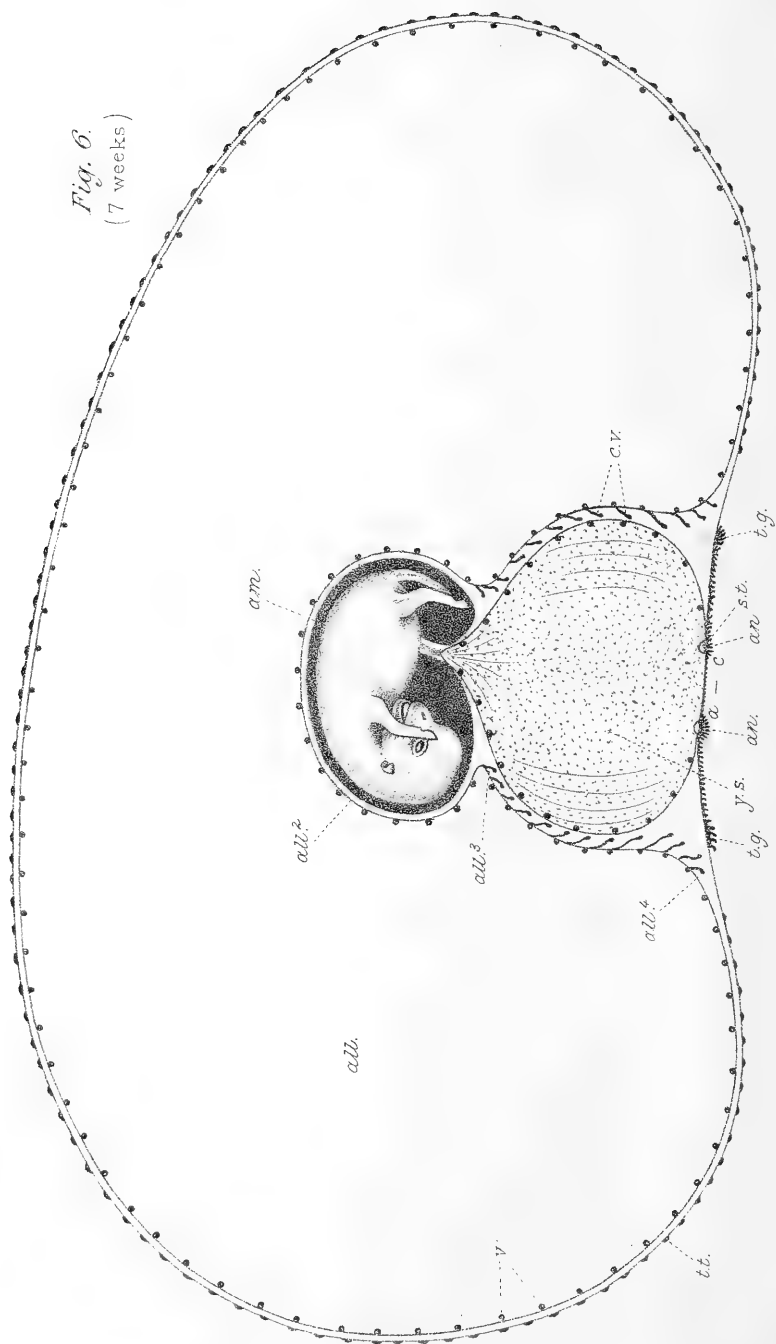


Fig. 3.
(4 weeks)



Fig. 6.
(7 weeks)



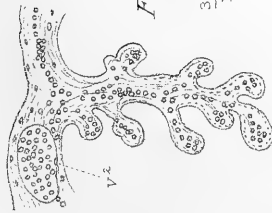


Fig. 7b

$$\frac{30}{1}$$

11

villus
at 16 weeks.

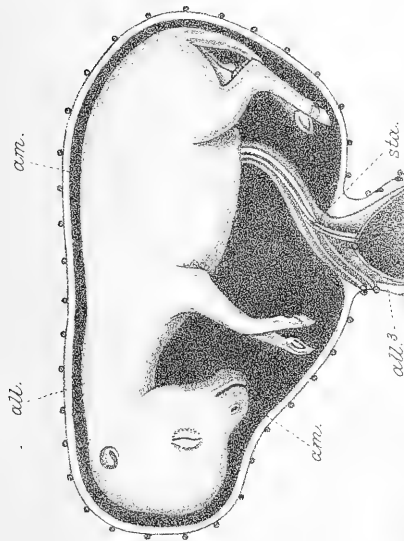


Fig. 7a

$$v^2$$

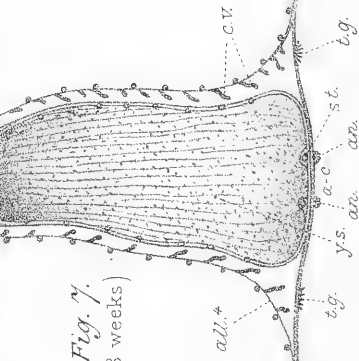
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317

villi at 8 weeks.



Fig. 7.
(8 weeks)



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